

Functionally important metabolic interactions between ectodermal and mesodermal tissue constituents have been described previously by other investigators.^{19,20} The existence of a similar interaction for the maintenance of protein formation in cells with relatively low oxidative metabolism by another cell type with a different metabolic pattern could be of significance as a form of cell interaction occurring during embryonic development. Experiments designed to explore more extensively such a possibility are in progress at this laboratory.

Thanks are due Mrs. M. Cooper for her able assistance in carrying out the experiments.

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SPECTRAL LUMINOSITY CURVES FOR PROTANOPIC, DEUTERANOPIC, AND NORMAL SUBJECTS*

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The luminosity curve shows how the sensitivity¹ of the eye varies for various wave lengths. Sensitivity is measured in terms of the reciprocal of the energy required to produce a given effect—threshold, for example.

In 1952 we published an article on the foveal luminosity curves of five normal subjects.² The present account is concerned with the spectral sensitivity curves of two groups of color-blind subjects,³ five protanopes and six deuteranopes, as compared with the curves obtained on seven normal subjects. Until the work of Hecht

and Hsia⁴ it was not considered that deuteranopes show a loss of cone sensitivity, as compared with normal subjects, in any part of the spectrum. Hecht and Hsia found, on calculating sensitivities based on the computed energies of their filtered lights, that deuteranopes seem to show a loss of sensitivity in the green region of the spectrum. They emphasized the fact that some earlier results which seemed to show no loss of green sensitivity in deuteranopes could be due to the prevalent practice of plotting per cent values of sensitivity rather than values based on energy.⁵

The present experiments have been performed to investigate, by improved techniques, the still not universally accepted fact of cone luminosity losses in deuteranopes. We have also obtained threshold luminosity data on a small group of protanopes. Our results show that, as compared with normal subjects, both types of color-blind individuals demonstrate sensitivity losses; five of the six deuteranopes show a deficit of luminosity in the green-to-blue part of the spectrum, and all the protanopes show a loss in the red.

Subjects.—For our measurements we used five protanopes and six deuteranopes. Our seven normal subjects consisted of the five whose foveal data have been described earlier² plus two additional ones, a man and a woman, each about twenty-five years of age.

The testing of all subjects involved the reading of the Ishihara and Stilling plates, the determination of the proportion of red and green required to match a yellow on the Hecht-Shlaer anomaloscope,⁶ and the determination of the neutral point in the spectrum. The tests are all highly discriminative for the three classes of individuals studied—normal, protanopic, and deuteranopic.

The color-blind subjects were all complete dichromats. We first chose those persons who made extensive errors in the Ishihara and Stilling tests. Of these, we selected only those who in the anomaloscope were able to match perfectly the yellow of 575 m μ with a green of 555 m μ by itself and also with the red of 635 m μ by itself. By comparing the relative luminances at match of the yellow and red, we classified the subject as protanopic or deuteranopic. If the red luminance required by a subject was disproportionately greater (to a normal eye) than the yellow, that subject was called a protanope, whereas if, at match, the red and yellow were approximately equal, he was called a deuteranope. The final critical test was always to determine the presence in the spectrum of a neutral point (the narrow wavelength band seen as white by dichromats). Only those subjects who matched a sharply located neutral point with white light of 5,000° K. as a standard were considered to be complete dichromats. The neutral-point determinations were made with a modified Helmholtz color mixer.⁷

Apparatus and Procedure.—Our observations involved the use of a double monochromator whose light could be varied by the use of appropriate controls with respect to wave length, energy, duration, and subject's retinal position. The energy measurements were done with a photronic cell (Weston, Model 594 RR, at the pupil position) and a moving-coil galvanometer. The apparatus, essentially a Maxwellian view system, was in all details similar to the one described earlier.²

We found the subject's threshold at each wave length tested. Our test field was a circular one subtending a visual angle 42 minutes of arc in diameter. The test field was viewed by the subject's dark-adapted eye and appeared in the center of a fixation ring, i.e., a thin, dim ring of white light that subtended a visual angle 2.5°

in diameter. The duration of each single stimulus exposure was 4 milliseconds.

At the beginning of each session, the subject was dark-adapted for 10 minutes, presumably a sufficient time for the cones to gain full sensitivity. The subject presented each spectral light to himself by releasing a key. Presentations were so arranged that the light stimulations were in accord with the method of limits, three ascending and three descending series being given for each threshold determination. Three such thresholds, each one on a different day, usually provided the final data for the subject's average threshold at a given wave length.

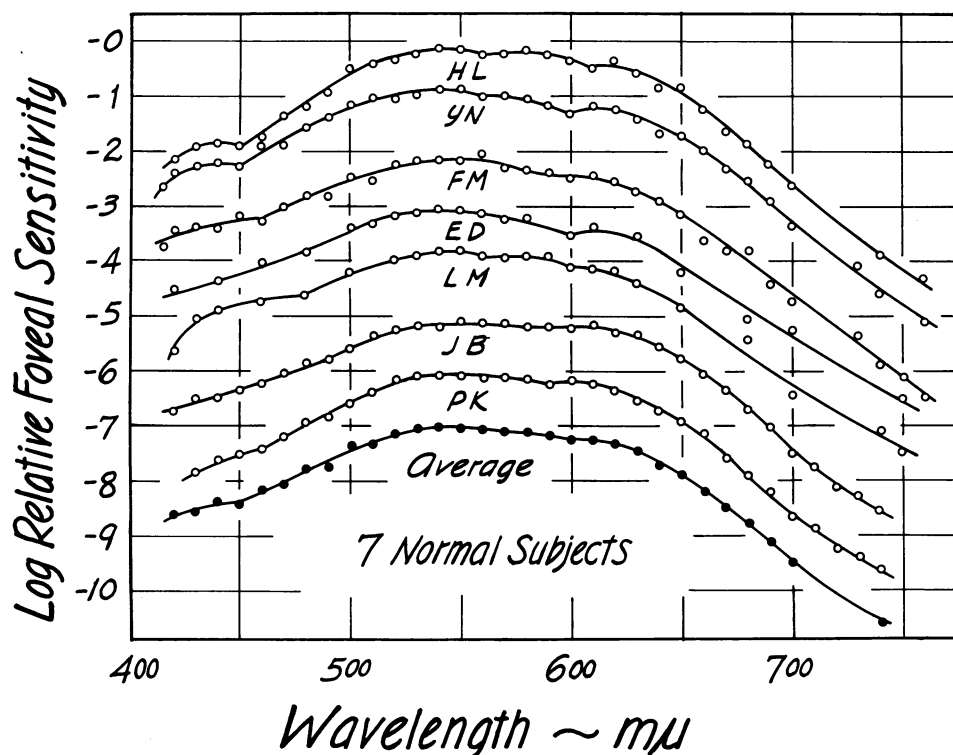


FIG. 1.—Log sensitivity curves as a function of wave length for seven normal subjects. The average curve is given at the bottom of the figure.

Results on Normal Subjects.—Figure 1 gives the individual log sensitivity curves for our seven normal subjects; the bottom curve presents the averaged data.⁸ The basic data of these curves are relative energies required for the cones to respond to the spectral lights at the absolute threshold; the logarithms of the reciprocals of these values (i.e., log sensitivity values) are here plotted. The peak of the average curve is arbitrarily set at zero (i.e., maximum sensitivity is set at unity). For purposes of clarity of presentation, each successive curve is moved downward through one logarithmic unit. The absolute energies may be computed by observing that at 578 $m\mu$ the average normal threshold (interpolated) is 3.5×10^{-8} erg, or about 10,000 quanta.

It is probably not necessary to labor the fact of the "humps" in the blue and in the orange, near 450 and 610 $m\mu$. Presumably in the normal subject they are manifestations of three (or more) primary processes.

Results for the Protanopes.—Figure 2 gives the luminosity curves for five protanopes. Each curve represents the data for an individual, and the average curve is given at the bottom of the graph.

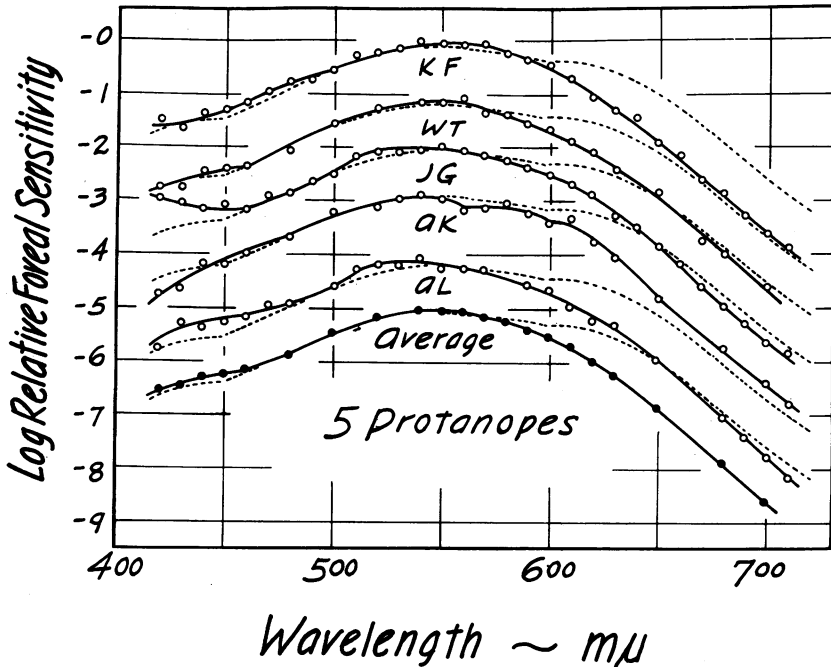


FIG. 2.—Log sensitivity curves for five protanopes. The average curve for normal subjects is drawn relative to each protanope's curve, so that log sensitivities are equated at 500 $m\mu$.

Since the thresholds for a given protanope over the spectrum may represent a higher or lower level of sensitivity than that represented by the average curve for normal subjects, it is desirable that each protanope be compared, not with the average normal subject, but rather with a normal subject whose sensitivities are, as it were, equivalent in those regions of the spectrum not affected by the condition of protanopia. On this basis the average curve for normal subjects has been drawn (dotted lines) relative to the curve for each protanope, the curve for normal subjects being so placed on the ordinate axis that the value of the log sensitivity at 500 $m\mu$ is set equal to the value lying on the curve for each protanope at that wavelength.

It is to be observed that the curve for each protanope indicates a greatly increased energy requirement in the red part of the spectrum. The protanope loses luminosity at long wave lengths.

Results for the Deuteranopes.—Figure 3 gives the results for the deuteranopes. Each single curve is the luminosity function for a single deuteranope. The average curve is presented at the bottom of the graph. The average curve for the normal

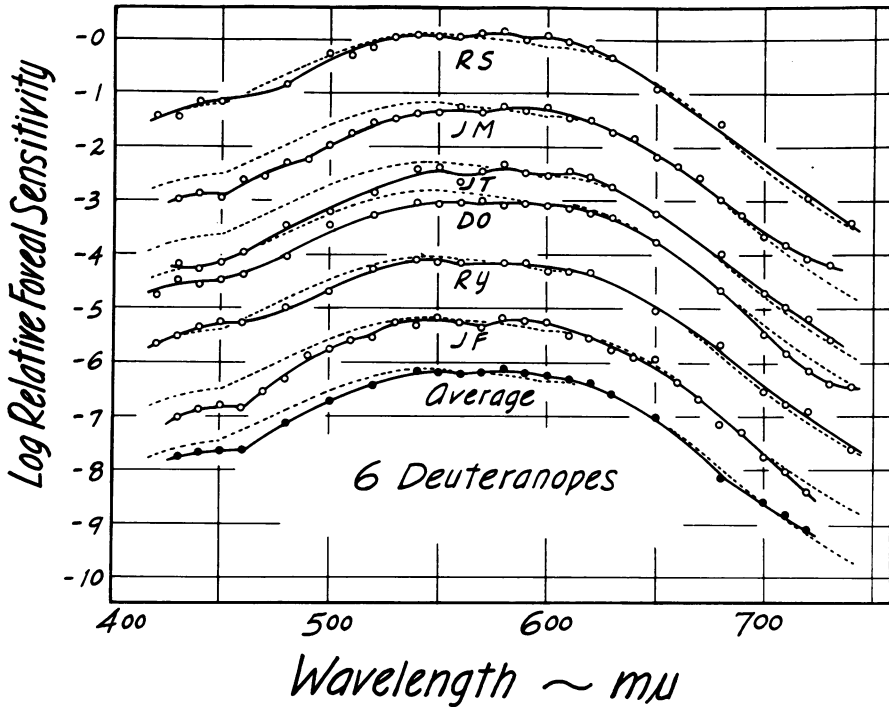


FIG. 3.—Log sensitivity curve for six deuteranopes. The average curve for normal subjects is so placed relative to each deuteranope's curve that log sensitivities are set equal at 650 $m\mu$.

subjects (dotted lines) is drawn relative to the curve for each deuteranope in such a way that the log sensitivity at 650 $m\mu$ for the normal curve is set equal to the value at that wave length for the given deuteranopic curve.

As shown by the single curves for the deuteranopes and the associated curves for normal subjects, it would seem that, in general, the deuteranope shows a normal luminosity in the red but a loss in the green and blue. (On an arithmetic plot of sensitivity, the degree of absolute loss would be greatest in the green.) The extent of the loss varies from subject to subject, and in one case (RS) a loss cannot be demonstrated.

The existence of the single deuteranope who, by our standards, does not show a significant loss may raise a question: Does the loss that seems to be usual in deuteranopia, as shown by its existence in five of our six subjects, exhibit a determinative character, or is it a correlated but not causative condition? We are in no position to discuss this matter and will only repeat what we have said previously: luminosity loss seems to be a usual condition in deuteranopia.

Summary of Results for All Groups.—Figure 4 and Table 1 summarize the average data for normal subjects as well as for the protanopes and the deuteranopes. The data, as presented in Figure 4, directly represent average log sensitivity values for all groups; no arbitrary adjustments along the ordinate axis have been made.

In general, one can say that the normal curve is a broad function that encompasses the extremes of the color-blind curves. Protanopes have nearly normal luminosity in the blue but show loss in the red; deuteranopes show normality in the

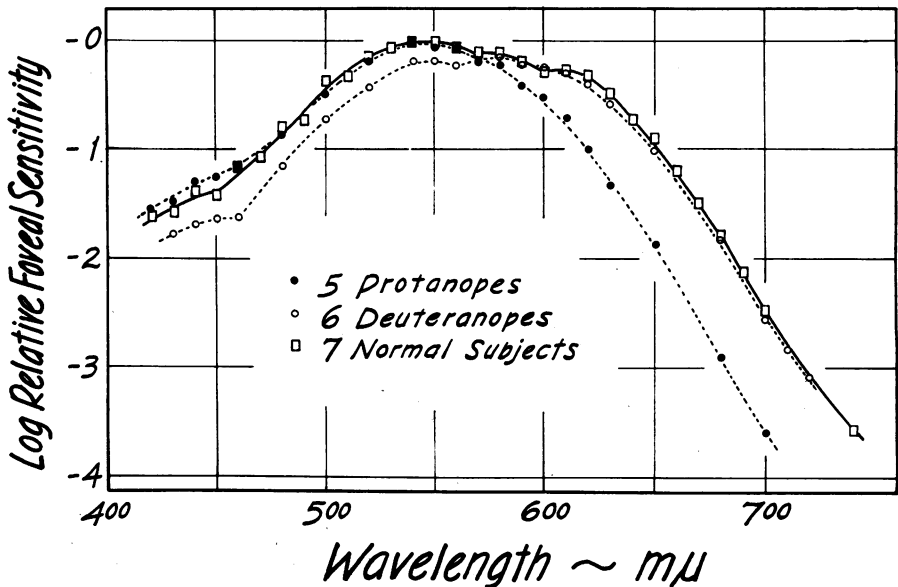


FIG. 4.—Average log sensitivity curves for the protanopes, deuteranopes, and normal subjects.

red but, in five out of six cases, a loss in the green and blue. The manner in which the two average functions cross as they take up their regions of normal luminosity provides an interesting picture; the protanope loses luminosity in the spectral region, where the deuteranope shows normal sensitivity. Conversely, the deuteranope loses sensitivity in the region where the protanope is normal.

The average curve for protanopes appears to be above the curve for normal subjects in the blue part of the spectrum. This apparent increase in luminosity is almost certainly not real; it depends almost completely on a single subject, JG, whose luminosities in the blue seem relatively high.

Humps in various luminosity curves might be expected to appear more clearly in individual curves than in averaged data. It is nevertheless true that the normal curve of Figure 4 shows a well-marked hump near 450 mμ and probably another in the region near 575 to 600 mμ. The latter hump seems to be definitely smoothed out in the curve for the protanopes, and the green peak near 540 mμ is diminished for the deuteranopes. The blue hump is, relatively, not conspicuously affected in the latter case.

Discussion.—Through the years since the time of Young,⁹ it has been supposed that protanopia is due to the loss of what we may call R-receptors, those that are especially sensitive to red. On the other hand, it has not generally been accepted that deuteranopia is due to a loss of G-receptors, those that are especially sensitive to green.

Because the evidence did not seem to support an interpretation of loss for the deuteranope, another sort of account seemed to be required for this type of color defect. The most widely held theory of deuteranopia has entailed the idea of a "transformation" system, as first described by Leber¹⁰ and by Fick.¹¹ One can think of the transformation system as representing a failure of the R- and G-receptors to

TABLE 1*

AVERAGE LOG₁₀ RELATIVE ENERGY VALUES FOR SEVEN NORMAL, FIVE PROTANOPIC, AND SIX DEUTERANOPIC SUBJECTS

Wave Length (Mμ)	Normal Subjects	Protanopes	Deuteranopes
420	1.61	1.53	..
30	1.57	1.47	1.77
40	1.39	1.29	1.68
50	1.42	1.24	1.63
60	1.17	1.16	1.62
70	1.07
80	0.80	0.85	1.15
90	0.73
500	0.38	0.48	0.72
10	0.33
20	0.15	0.17	0.44
30	0.07
40	0.01	0.02	0.19
50	0.02	0.07	0.18
60	0.06	0.05	0.22
70	0.11	0.18	0.20
80	0.12	0.22	0.14
90	0.19	0.41	0.22
600	0.28	0.53	0.24
10	0.27	0.71	0.32
20	0.32	1.00	0.40
30	0.48	1.27	0.58
40	0.73
50	0.89	1.87	1.01
60	1.20
70	1.50
80	1.79	2.91	1.83
90	2.13
700	2.49	3.60	2.58
10	2.83
20	3.10
30
40	3.58
50
60

* Concerning the data of individuals, see fn. 8. The absolute energy value for the average normal subject 578 mμ (interpolated) is 3.5×10^{-8} erg, equivalent to about 10,000 quanta at the cornea.

become differentiated from each other. They are presumed to have similar absorption characteristics but different central connections. The result would be that red, for example, would stimulate both central R- and G-systems. Since R and G produce yellow, it would be expected that the deuteranope would call all long wave lengths yellow, a response that is, in fact, in accord with what a unilaterally deuteranopic person sees in his color-blind eye: all long wave lengths are yellow. This yellow can be compared with what is seen in the normal eye.¹²

It must be understood that the transformation theory is applicable to protanopia as well as to deuteranopia. It has not been applied in the former case because of the fact that most workers seem to have accepted the principle of luminosity loss in protanopia. However, it should be noted that the narrowing of the classically drawn luminosity curve in protanopia could just as well be taken to be due to a "transformation" shift in absorption of the R-receptors toward that of the G-receptors.

The present result and that of Hecht and Hsia⁴ raise problems for the Leber-Fick type of theory.^{10, 11} There is a loss of green luminosity in a manner inconsistent with the latter theory. On the other hand, if we accept the fact of loss, how can

we account for a deuteranope's seeing of yellow, when, instead of G's absorption characteristics being "transformed" to those of R, G-receptors are lost, at least to a considerable extent?¹³

The present experiment gives no answer to the problem. A next step in analysis may profitably involve research on a unilaterally dichromatic subject; for, in the past, data on such subjects have not usually been extensive. We have been fortunate to obtain the services of a unilaterally dichromatic subject with a deficiency of spectral sensitivity primarily in the green. Reports of experiments on this subject will appear soon.

Summary.—Data have been obtained on three groups of subjects, made up, respectively, of five protanopes, six deuteranopes, and seven normal subjects. As compared with normal subjects, protanopes show a loss of luminosity in the red. In contrast with some previous interpretations but in conformity with the results of Hecht and Hsia,⁴ five of the six deuteranopes show a loss of luminosity in the green.

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Preliminary accounts in abstract form of the present experiment have appeared in C. H. Graham and Y. Hsia, *Proc. Fourteenth Intern. Congr. Psychol.*, p. 114, 1954; also *Science*, **120**, 780, 1954.

We are indebted to Professor Lucy J. Hayner, of the Physics Department, Columbia University, and Dr. Simon Shlaer, of the University of California, for technical discussions concerning our equipment.

¹ The terms *sensitivity* and *luminosity* as here used are synonymous with each other and with the terms *luminous efficiency* and *visibility*.

² Y. Hsia, and C. H. Graham, these PROCEEDINGS, **38**, 80, 1952.

³ Protanopes and deuteranopes are two classes in a larger class called "dichromats." The class of dichromats comprises, in addition to protanopes and deuteranopes, people in a rare class called "tritanopes" and those in a still rarer class called "tetartanopes." Dichromats can match any color of the spectrum by a mixture of two colors. Protanopes confuse red and green and show a loss of sensitivity in the red part of the spectrum. Deuteranopes also confuse red and green but require amounts of these two colors to match yellow that are different from those required by the protanopes. Tritanopes confuse blue and green. Tetartanopes also exhibit confusions between blue and green, but, unlike the other dichromats, who match a narrow region of the spectrum with white, the tetartanopes match two regions of the spectrum with white.

⁴ S. Hecht and Y. Hsia, *J. Gen. Physiol.* **31**, 141, 1947.

⁵ For example, see F. H. G. Pitt, *Great Britain Med. Research Council Special Rept. Ser.*, No. 200, 1935.

⁶ For a discussion of the Hecht-Shlaer anomaloscope see M. P. Willis and D. Farnsworth, *Med. Research Lab., U.S. Naval Submarine Base*, Vol. 11, No. 7, Rept. No. 190, 1952. References to the Ishihara and Stilling tests are as follows: S. Ishihara, *Tests for Colour-Blindness* (6th ed.; Tokyo: Kanehara, 1932); E. Hertel, *Stillings pseudo-isochromatische Tafeln* (Leipzig: Georg Thieme, 1936).

⁷ S. Hecht and S. Shlaer, *J. Gen. Physiol.*, **20**, 57, 1936.

⁸ The numerical data of individual subjects, color-blind and normal, have been deposited with the American Documentation Institute (order Doc. No. 5366 from ADI Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington 25, D.C., remitting in advance \$1.25 for microfilm or \$1.25 for photocopies. Make checks payable to Chief, Photoduplication Service, Library of Congress.

⁹ T. Young, "On the Theory of Light and Colours," in *Lectures in Natural Philosophy*, **2** (London: Joseph Johnson, 1807), 613.

¹⁰ T. Leber, *Arch. Ophthalmol.*, **15** (3), 26, 1869.

¹¹ A. Fick, "Die Lehre von der Lichtempfindung," in *Handbuch der Physiologie*, ed. L. Herrmann, 3, Part 1 (Leipzig: Vogel, 1879), 139.

¹² See, on the topic of unilaterally color-blind persons, the discussion by D. B. Judd, *J. Research Nat. Bur. Standards*, 41, 247, 1948.

¹³ For strong objections to the idea of luminosity loss in deuteranopia see G. L. Walls, and R. W. Matthews, *Univ. Calif. Publ. Psychol.*, Vol. 7, 1952.

ON SOME PHENOMENA IN DROSOPHILA RELATED TO
SO-CALLED GENIC CONVERSION

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While analyzing the action of the rudimentary locus (r , 1, 54, 5),¹ many backcrosses were made involving one X-chromosome marked with Bar (B , 1, 57.0), with or without additional markers, and the rudimentary alleles r^9 and r^{39} , the latter carrying also Bar and forked (f , 1, 56.7). In view of the \pm sterility of rr females, the backcrosses were always $(B/B \text{ } \varnothing \times r \sigma^7) \times r \sigma^7$, which gives $1/2$ females rr , $1/2$ females $+B/r+$, $1/2$ males B , $1/2$ males r . The variations of this general scheme were the use of r^9 or r^{39} f B males. All combinations were made, viz., $(B \times r^9) \times r^9$, $(B \times r^9) r^{39}$, $(B \times r^{39}) r^9$, $(B \times r^{39}) r^{39}$. In addition, five different chromosomes with B were used, three of them kept over different crossover inhibitors. The unexpected results we obtained in 6 out of more than 400 $R \text{ } F_2$, 5 in $(B^{St} \times r^9) \times r^{39}$ 1 in $(B^{Pas} \times r^9) r^9$. (The number of normal backcrosses has increased considerably since, without a repetition of the unexpected findings.)

The First Group.—From the Bar stock which we designate as B^{St} (not containing crossover inhibitors) single females were crossed to r^9 males and eleven F_1 females, partly sisters, partly not, backcrossed individually to r^9 males. All results were as expected. Eight more females of the same provenience were backcrossed to r^{39} f B males. The results of three matings were again according to expectation (see Table 1). The somewhat irregular crossover classes may be chance happenings. The over-all value of 3.5 per cent crossovers is about normal (2.5 map distance

TABLE 1
 $RF_2 (B^{St} \times r^9) \times r^{39}$ f B PHENOTYPES

No.	\varnothing			σ^7			
	B/B	$B/+ \text{ } r/r$	$B/B \text{ } r/r$	B	r	rB	$+$
4572	101	91	3	62	42	19	1
4573	54	69	1	59	52		1
4574	78	72	4	71	70		1
S.	233	232	8	192	164	19	3
4566	66		45	16		40	
4568	43		54	43		40	
4569	39	10	40	31	3	34	
4570	54	4	39	51	5	46	
4571	71	2	76	60		64	
S.	273	16	254	201	8	224	